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Comparison of prenatal and postnatal ontogeny: cranial allometry in the African striped mouse (*Rhabdomys pumilio*)

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The relationship between prenatal and postnatal ontogenetic allometry is poorly known, and empirical studies documenting prenatal allometry are few, precluding an understanding of changes in growth patterns during life history and their relation to proximal, physiological, and ultimate evolutionary variables. In this study I compare prenatal and postnatal ontogenetic allometry of the cranium in a cleared and stained developmental series of the African striped mouse (*Rhabdomys pumilio*). Eighteen cranial measurements, reflecting the dimensions of individual elements, were analyzed using bivariate and multivariate estimates of allometry and methods of matrix comparison. Prenatal allometry is characterized in *R. pumilio* by a relative rapid lengthening of cranial elements, particularly the frontal, parietal, basisphenoid, premaxilla, and palatine, as evidenced by larger bivariate allometric coefficients (>30% increase) and, across all variables measured, a greater proportion of cranial elements growing with a positive allometry than in the postnatal period. Growth dynamics are found to shift for measurements of several elements including the parietal, frontal, and palatine, indicating a nonlinearity of ontogenetic allometry with respect to birth; similar shifts have been found between prenatal and postnatal growth for some regions of the human cranium. Application of common principal component analyses, a generalized extension of principal component analysis, revealed that the prenatal and postnatal matrices shared a highly similar structure, further quantified by high correlations (>0.78) using the random skewers method of matrix comparison. These results indicate a close correspondence between morphology-based variance structures over the course of ontogeny in *R. pumilio*.

Key words: common principal components, cranium, growth, ontogenetic allometry, ontogeny, prenatal allometry, random skewers, *Rhabdomys*, rodent

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Morphological changes in evolution do not happen simply at the adult stage; ontogenetic pathways evolve too. Stemming from the early 20th century (Gayon 2000), an extensive amount of literature has clarified morphological differences in a developmental context by the examination of covariation among traits across ontogenetic stages of a given species, commonly termed ontogenetic allometry (Cock 1966; Klingenberg 1998). A recent resurgence in the investigation of ontogenies has been facilitated by the advent and application of analytical techniques and metric methods, which have permitted differences in form to be appreciated quantitatively and intuitively.

Although much study has been directed to documenting the variability and evolution of ontogenetic allometry in mammals—for instance detailing the relation of diet to growth patterns (Beecher and Corruccini 1981; Corruccini et al. 1985), examining how growth patterns are influenced by environmental conditions (Fadda and Leirs 2009) or exhibit heterochronic patterns (Cubo et al. 2006; Weston 2003; Zollikofer and Ponce de León 2004, 2010), and investigating growth patterns among species and clades (Cardini and O'Higgins 2005; Creighton and Strauss 1986; Marroig 2007; Wilson and Sánchez-Villagra 2010) – all of these works have dealt with the postnatal period of development. Despite recognition that early ontogenetic stages are an important component of influence on adult morphology (Bastir and Rosas 2004; Bulygina et al. 2006; Wilson et al. 2008, 2010a; Viðarsdóttir et al. 2002), studies of prenatal allometry in mammals are scarce and, with the exception of a study on the common European mole (Goswami and Prochel 2007), are limited to humans (Bastir and Rosas 2009; Latham 1972; Mandarim-de-Lacerda and Alves 1992; Plavcan and German

1995; Sardi et al. 2007; Vinicius 2005). The relationship between prenatal and postnatal allometry is poorly known, and the role that prenatal allometry plays in providing raw material for morphologic evolution currently cannot be evaluated. One reason for this is the difficulty in obtaining prenatal developmental series for any mammal with the sample size required to assess allometric relationships (Sánchez-Villagra 2010).

Several studies of skull growth in rodents have indicated that postnatal ontogenetic allometry is nonlinear for some species, including model organisms such as the house mouse and cotton rat, and that ontogenetic trajectories stabilize during the postnatal period, at about the time of weaning (Hingst-Zaher et al. 2000; Willmore et al. 2006; Zelditch 1988; Zelditch and Carmichael 1989; Zelditch et al. 2003). The adult pattern of cranial integration exhibited by preweaning rats reflects the influence of functional and developmental sources of constraint, and experimental studies using rats have revealed that the preweaning period plays a critical role in the development of normal skull shape (Pucciarelli and Oyhenart 1987). Nevertheless, in contrast to these results, several studies on other mammalian species, including rodents (Monteiro et al. 1999), primates (O'Higgins et al. 2001; Singleton 2002), and hippopotamuses (Weston 2003) have suggested that ontogenetic allometry is linear. Complexity is added to this debate because during the prenatal period the embryo is not in a forceless environment (Harris et al. 1981; Tuckett and Morriss-Kay 1985), and throughout later prenatal stages movements occur that are equivalent to those happening after birth (Hamburger 1973). Hence, although postnatal ontogenies represent at least the possible pathways that can be taken to reach a realizable adult form through development, it remains unclear how early in development these pathways are fixed. Especially given the complex interactions between genetic and epigenetic factors that control skull morphogenesis (Herring 1993), with epigenetic factors also influencing prenatal growth, for example, in embryonic muscle-loading (Atchley et al. 1984; Hall 2005), it is clear that framing cranial growth in a more extended context that incorporates the earliest periods of development is necessary. Particularly, the finding that life-history and developmental milestones are correlated with alterations to covariance structure during postnatal cranial growth in rats and humans leads to the expectation that birth also might represent a point of significant transition in growth dynamics (Mitteroecker and Bookstein 2009).

The objective of this study is to document prenatal allometry for a nonmodel rodent species and compare this with postnatal allometry to provide an estimation of the relationship for growth dynamics of cranial elements between the 2 periods, separated by birth. A developmental series of cleared and stained specimens of the African striped mouse (*Rhabdomys pumilio*) is used as subject for investigation. Found from Uganda and Kenya to Angola and South Africa, *R. pumilio* is a diurnal murid rodent that attains approximately twice the body mass of the house mouse (*Mus musculus*—Wilson and Reeder 2005). *R. pumilio* has been the subject of several ecological studies because it has a complex and fluid social system and has been shown to demonstrate parental care in laboratory and desert populations (Schradin and Pillay 2003, 2004).

Table 1.—Osteological measurements recorded in the present study.

Orientation of specimen	Variable	Abbreviation
Lateral	Jugal length	JUL
	Squamosal length	SQL
Ventral	Premaxilla length	PRL
	Premaxilla width	PRW
	Maxilla length	MXL
	Palatine length	PLL
	Palatine width	PLW
	Basioccipital length	BOL
	Basisphenoid length	BSL
	Basioccipital width	BOW
	Basisphenoid width	BSW
Dorsal	Nasal length	NAL
	Nasal width	NAW
	Frontal length	FRL
	Minimum interorbital width	MIW
	Skull length	SKL
	Parietal length	PAL
	Parietal width	PAW

Materials and Methods

Specimens and preparation.—I measured an ontogenetic series of 56 specimens of *R. pumilio*, comprising 25 prenatal individuals and 31 postnatal specimens. All of the prenatal specimens and 16 of the postnatal specimens were obtained from breeding colonies maintained for research at the Universität Zürich (Schradin 2006) and were prepared using a modified version of standard enzymatic clearing and double staining (Wilson et al. 2010b). The founder individuals of *R. pumilio* originated from the Geogap Nature Reserve in South Africa (29°41.56′S, 18°1.60′E). The remaining 15 postnatal specimens in the study sample included adult and juvenile crania measured from the osteological collections at the Universität Zürich. For each of the cleared and stained specimens ($n = 41$) the crown–rump length (CRL) was measured from digital photographs taken of the whole animal before preparation, using a Leica M165C microscope (Leica, Heerbrug, Switzerland) and camera attachment. The CRL ranged from 14.8 to 41.1 mm, which equates to approximately 16.5 days postconception to 2 postnatal days of age (Kaufman 2008).

Data collection.—Eighteen measurements were recorded from each cranium (Table 1; Fig. 1). These were chosen to record the dimensions of single bones rather than encapsulating several bones. This approach was adopted to enable the allometry of a single element to be identified, and also because many elements are not ossified completely in prenatal specimens, and hence portions of the skull include cartilag-

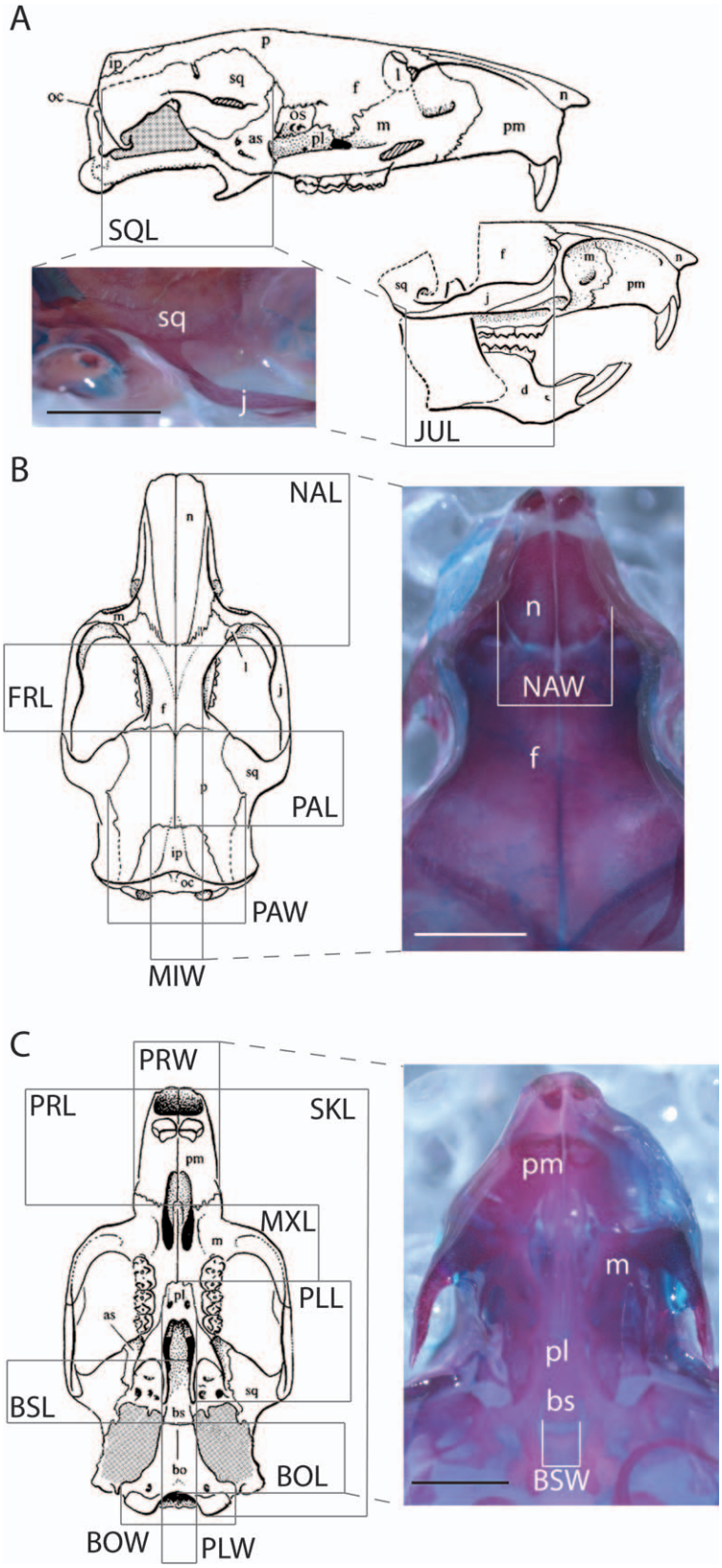

Fig. 1.—Illustrative guide for the cranial measurements recorded from cleared and stained crania of *R. pumilio* in A) lateral, B) dorsal, and C) ventral orientations. Scales: 2 mm. Abbreviations of measurements are given in Table 1. Labeled elements: nasal (n), maxillary (m), jugal (j), lacrimal (l), frontal (f), parietal (p), squamosal (sq), interparietal (ip), occipital (o), premaxillary (pm), palatine (pl), alisphenoid (as), basisphenoid (bs), basioccipital (bo), dentary (d), orbitosphenoid (os). Modified after Wilson and Sánchez-Villagra (2009).

inous regions that make the recording of measurements spanning across several bones difficult. A reflex microscope was used to record 3-dimensional landmarks on all cleared and stained specimens. This method was 1st applied by Goswami and Prochel (2007), who used reflex microscopy to gather data from cleared and stained common European moles (*Talpa europaea*). Often used in the fields of dentistry and component manufacture, reflex microscopy is especially useful because it affords the possibility to measure small and delicate materials, such as embryos, with a resolution of approximately 1 μm. Each specimen was suspended in glycerol in a sampling dish and held in position using pins fixed to a dissection mat. A total of 108 landmarks were digitized in dorsal, ventral, and lateral orientations. Measurements were computed from 3-dimensional coordinates, and adult and juvenile osteological specimens were measured with digital calipers. In both instances measurements were computed from an average of 3 repetitions for each variable. Measurement error was 0.034 mm for landmarks obtained using the reflex microscope, and 0.09 mm for measurements taken using digital calipers.

Bivariate allometry.—Two matrices were constructed, 1 for the prenatal specimens ($n = 25$) and 1 for the postnatal specimens ($n = 31$). Bivariate allometry was estimated for each matrix using skull length and CRL (for cleared and stained specimens) as proxies for body size. Skull length and CRL were regressed against one another, because skull length can scale allometrically with true body size, and CRL is a commonly accepted body size metric for embryological specimens. To study the scaling relationships between cranial variables I used the linear transformation ($\log_{10}$) of the power equation $y = b_0 x^{b1}$ where y is the variable of study, b_0 is the y-intercept, x is a proxy for size, and the coefficient b_1 details the relative magnitude of y versus x change, thus indicating ontogenetic polarity. When $b_1 = 1$ the 2 traits under study change only by means of absolute size; that is, isometric growth ($y/x = b_1$). If $b_1 < 1$, y is negatively allometric in respect to x, and if $b_1 > 1$, y is positively allometric with respect to x (i.e., with growth the ratio y/x increases). The independent variable was normally distributed (Shapiro-Wilk test, $w = 0.231$, $P = 0.209$), thus 2-tailed *t*-tests were used to assess the significance of deviations from isometry, whereby type I error rate (α) was fixed at 0.01 under the null hypothesis of $b_1 = 1$. A relationship was deemed isometric if not significantly different from unity. To improve the reliability of estimates allometric coefficients (b_1) were calculated using both least-squares (LS) and reduced major axis (RMA) regression methods (model I and II). Symmetrical line-fitting techniques (model II), such as RMA, usually are preferred (Wolpoff 1985) because error is assumed to be associated equally with both x and y variables, and simulation investigations have indicated these methods provide more stable estimates, especially if sample sizes are small (Riggs et al. 1978). In contrast, LS assumes that the independent *x* variable is measured without error. When this assumption is violated, LS estimates consistently will underestimate the true slope, because by definition RMA = LS/*r* with $r \leq 1$, and the magnitude of this error will increase with decreasing correlation (*r*) between the variables (Harvey and Pagel 1991).

Multivariate allometry.—In multivariate allometry (Jolicoeur 1963) an allometric trajectory is represented by the 1st eigenvector (axis) of a principal component analysis (PCA) using the covariance matrix of natural log-transformed measurements. Because PCA requires a complete data set, it was necessary to remove several specimens that had measurements missing for a variable, and hence the prenatal matrix contained 17 specimens and the postnatal matrix 25 specimens. To prevent a singular matrix from being produced, only 14 of the 18 measured variables were included in the multivariate analyses. The coefficients of the 1st principal components (PC1s) for each of the 14 variables were used to identify growth trends by comparison to the isometric vector of length (*p*): the value at which all PC1 coefficients are equal, calculated as $p^{-1/2}$ (where p = number of measured variables). The bootstrap approach was used to compute standard error (*SE*) values for PC1 coefficients in comparison with the value expected for isometry; replicates were performed for 1,000 iterations for each matrix (Efron and Tibshirani 1993). A growth trend was identified to be positively or negatively allometric if the bootstrap confidence interval for the PC1 coefficient did not include the isometric vector.

Vector and matrix comparisons.—I used common principal component (CPC) analysis (Flury 1988) and the random skewers method (Cheverud 1996) to compare the structure of the prenatal and postnatal covariance matrices. Because specimens were pooled into these 2 matrices, changes in covariance structure within each group, and their potential effects, cannot be determined. This sacrifice was made simply to permit a comparison that low sample size would disallow if individual stages were evaluated, and for this reason the results are not directly comparable with studies that document how integration changes over the course of ontogeny. CPC and random skewers methods differ fundamentally in that CPC analysis considers a null hypothesis of equality among covariance matrices, but the random skewers method assumes a null hypothesis of no structural similarity. CPC analysis is a generalization of a single PCA to multiple groups and permits the sharing of complex relationships between covariance matrices (Flury 1988). Relationships between matrices are tested following a hierarchy that begins with unrelated structure and ends with equality and is based upon the understanding that if 2 matrices share 2 PCs, they necessarily share 1. As such, a number of hypotheses are considered by comparing eigenvectors and eigenvalues; equality—matrices share equal eigenvalues and eigenvectors; proportionality—matrices share equal eigenvectors and proportional eigenvalues; CPC—matrices share common PCs whereby the eigenvectors are equal but the eigenvalues are unequal; and unrelated structure—the 2 matrices have unequal eigenvectors and eigenvalues (Phillips and Arnold 1999). Because ontogenetic data are often nonnormally distributed, the likelihood ratio tests commonly used to evaluate the CPC models are not

TABLE 2.—Results of bivariate allometry analyses. r^2 = adjusted coefficient of determination, b_1 = coefficient of allometry, p^{iso} = *P*-value for null hypothesis of isometry (coefficient of allometry = 1), RMA = reduced major axis, LS = least squares. Definitions of osteological variables are provided in Table 1.

	Prenatal specimens (n = 25)										Postnatal specimens (n = 31)				
	Skull length					Crown–rump length					Skull length				
	RMA		LS			RMA		LS			RMA		LS		
Variable	b_1	p^{iso}	b_1	p^{iso}	r^2	b_1	p^{iso}	b_1	p^{iso}	r^2	b_1	p^{iso}	b_1	p^{iso}	r^2
JUL	1.70	0.0002	1.41	0.0181	0.69	1.65	<0.0001	1.43	0.0029	0.75	0.97	0.6366	0.89	0.1224	0.84
SQL	1.50	0.0036	1.24	0.1458	0.68	1.96	<0.0001	1.59	0.0030	0.66	1.32	0.0005	1.25	0.0059	0.89
PRL	1.32	0.0419	1.01	0.9672	0.78	1.17	0.2181	0.88	0.3855	0.57	1.52	<0.0001	1.42	0.0004	0.87
PRW	0.99	0.1530	0.50	0.0028	0.66	0.75	0.0671	0.55	0.0027	0.63	1.13	0.1460	1.03	0.6849	0.85
MXL	1.65	<0.0001	1.49	0.0002	0.82	1.49	0.0005	1.28	0.0371	0.73	1.19	0.0369	1.09	0.2965	0.84
PLL	2.60	<0.0001	2.44	<0.0001	0.88	2.08	<0.0001	1.88	<0.0001	0.81	0.83	0.0304	0.73	0.0014	0.78
PLW	0.73	0.0138	0.44	<0.0001	0.66	0.69	0.0026	0.39	<0.0001	0.62	1.11	0.4392	0.86	0.3265	0.70
BOL	1.05	0.6456	0.88	0.2234	0.70	0.96	0.6899	0.78	0.0257	0.66	1.05	0.4216	1.00	0.9739	0.90
BSL	2.60	<0.0001	2.44	<0.0001	0.88	2.40	<0.0001	2.02	0.0001	0.71	1.70	<0.0001	1.59	<0.0001	0.88
BSW	0.70	0.0059	0.40	<0.0001	0.73	0.70	0.0048	0.41	<0.0001	0.73	2.04	<0.0001	1.96	<0.0001	0.92
BOW	1.29	0.0079	1.14	0.1874	0.78	1.19	0.0599	1.02	0.8172	0.74	0.83	0.0470	0.72	0.0020	0.75
NAL	1.98	<0.0001	1.86	<0.0001	0.89	1.75	<0.0001	1.59	<0.0001	0.82	2.02	<0.0001	1.99	<0.0001	0.97
NAW	0.82	0.0006	0.77	<0.0001	0.90	0.73	<0.0001	0.67	<0.0001	0.83	0.38	<0.0001	0.34	<0.0001	0.78
FRL	1.42	<0.0001	1.31	0.0016	0.85	1.36	0.0018	1.18	0.0973	0.75	0.74	<0.0001	0.71	<0.0001	0.93
MIW	0.76	0.0001	0.68	<0.0001	0.81	0.84	0.0146	0.75	0.0003	0.79	0.25	<0.0001	0.18	<0.0001	0.72
PAL	1.33	0.0253	1.03	0.8112	0.70	1.14	0.2615	0.85	0.2263	0.55	1.50	<0.0001	1.43	<0.0001	0.91
PAW	1.23	0.0013	1.17	0.0121	0.91	1.16	0.1247	0.99	0.9233	0.73	0.37	<0.0001	0.34	<0.0001	0.84

suitable. Instead, I examined the angular difference between vector PCs of the individual matrices in comparison to CPCs, and also the amount of variance encapsulated in the individual PC1s compared to the CPC1s, to estimate the goodness of fit of the CPC model (Klingenberg and Zimmermann 1992). Although the possible number of CPCs that can be generated from analysis of the prenatal and postnatal matrices is 12 (calculated as $n - 2$; where n = number of variables), examination was limited to CPC(7), that is the sharing of the first 7 components, because in both the prenatal and postnatal matrices loadings beyond the 6th component were close to 0.

To assess the significance of angular comparisons I computed vector angles between 1,000 pairs of randomly generated unit length vectors. The angles calculated between these vectors were compiled, and the 1% quantile of this distribution was used to assess significance (<27.6°). All CPC analyses of prenatal and postnatal covariance matrices were conducted using CPC software (Phillips 1998).

To gain a clearer insight into the degree of similarity between prenatal and postnatal patterns of covariance the random skewers method was used in conjunction with CPC analysis. The latter has been shown to often diagnose matrices to be completely dissimilar, despite other matrix correlation tests depicting the opposite result (Steppan 1997). Simulated tests indicate that relatively restricted changes in causal structure will produce a result of complete matrix dissimilarity (Houle et al. 2002), and examining how well the constructed matrices match the original ones yields a more real estimate of model fit (Arnold and Phillips 1999). The random skewers method measures matrix similarity by correlating the selection response between 2 matrices using a series of random selection vectors, in this case 10,000. Vectors are drawn from a uniform distribution between 0 and 1, assigned positive or negative signs with a probability of 50%, and standardized to unit length. Each selection vector is applied to each matrix, and the vector correlations between the paired expected responses are compared. The outputted vector correlations are used to generate an average vector correlation, which is a measure of the covariance matrix similarity, and, associated with this, a significance value based on the distribution of correlation values (Cheverud 1996; Cheverud and Marroig 2007). The matrix constructed at each stage of the CPC hierarchy was compared to the original matrices using the random skewers method.

RESULTS

For several traits, bivariate and multivariate allometric analyses reveal differences in growth relationships between prenatal and postnatal animals. Matrix comparison tests indicate that these differences do not preclude a result of overall similarity in covariance structure between each of the 2 matrices.

Bivariate results.—For both prenatal and postnatal specimens RMA and LS regression approaches produced broadly similar allometric trends (Tables 2 and 3). Consistency between the 2 methods was highest for postnatal specimens, with maxilla length (MXL) being the only variable that differed between RMA and LS. For prenatal specimens 5 of the variables differed between RMA and LS when skull length was used as a proxy for body size (Table 3). Across the variables considerable differences in relationship to skull length were exhibited by both prenatal and postnatal specimens. These relationships were lower for prenatal

Table 3.—Gross comparison of bivariate results using reduced major axis (RMA) and least-squares (LS) regression. Symbols indicate isometry (=), positive allometry (+), and negative allometry (−). Definitions of osteological variables are provided in Table 1.

	Prenatal specimens				Postnatal specimens	
	Skull length		Crown–rump length		Skull length	
Variable	RMA	LS	RMA	LS	RMA	LS
JUL	+	+	+	+	=	=
SQL	+	=	+	+	+	+
PRL	+	=	=	=	+	+
PRW	=	−	=	−	=	=
MXL	+	+	+	+	+	=
PLL	+	+	+	+	−	−
PLW	−	−	−	−	=	=
BOL	=	=	=	=	=	=
BSL	+	+	+	+	+	+
BSW	−	−	−	−	+	+
BOW	+	=	=	=	−	−
NAL	+	+	+	+	+	+
NAW	−	−	−	−	−	−
FRL	+	+	+	=	−	−
MIW	−	−	−	−	−	−
PAL	+	=	=	=	+	+
PAW	+	+	=	=	−	−

specimens, varying between r^2 values of 0.66 ($F_{1,24} = 5.78$, $P = 0.003$) for premaxilla width (PRW) and 0.91 ($F_{1,24} = 7.05$, $P = 0.012$) for parietal width (PAW) using skull length, and 0.55 ($F_{1,24} = 9.33$, $P = 0.067$) for parietal length (PAL) to 0.83 ($F_{1,24} = 54.01$, $P < 0.001$) for nasal width (NAW) when using CRL, compared with postnatal specimens where the range is from 0.70 ($F_{1,30} = 40.62$, $P = 0.326$) for palatine width (PLW) to 0.97 ($F_{1,30} = 87.86$, $P < 0.001$) for nasal length (NAL; Table 2). CRL was significantly correlated with skull length for all prenatal specimens (0.84; $P < 0.001$), and regression results indicate skull length scales isometrically among the prenatal specimens using both RMA ($b_1 = 1.03$, $F_{1,24} = 46.16$, $P > 0.05$) and LS ($b_1 = 0.95$, $F_{1,24} = 46.16$, $P > 0.05$) methods. Hence for the prenatal specimens herein, skull length scales isometric with size.

The distribution of growth trends differed between prenatal and postnatal specimens. For prenatal specimens 11 (65%) of 17 variables exhibited significant positive allometry when using RMA, 4 exhibited significant negative allometry (24%), and 2 variables scaled isometrically with skull length (11%; Table 3). When using CRL as a body size proxy, 4 of the 11 aforementioned positive allometric trends (squamosal length [SQL], premaxilla length [PRL], basioccipital width [BOW], and PAL) were identified instead to be isometric, but the variables exhibiting negative trends were the same as those when the analysis was performed using skull length (PLW, basisphenoid width [BSW], nasal width [NAW], and minimum interorbital width [MIW]). Positive allometric trends were identified for fewer variables in postnatal specimens (7; 41%); a greater amount of negative (6; 35%) and isometric (4; 24%) trends exist (Table 3). Across all variables the average allometric coefficient for prenatal specimens was 1.39 compared with 1.12 for postnatal specimens, indicating a shift in the relative magnitude of growth rate between the 2 periods (Table 2). For several variables, including basisphenoid length (BSL), frontal length (FRL), and PAW, coefficients were ≥30% greater for prenatal specimens (Fig. 2; Table 2). When comparing between prenatal and postnatal specimens, the 2 groups share the same growth trends for 59% (10; 6 positive, 2 negative, and 2 isometric trends) of the variables, using RMA and skull length (see Fig. 2A as an example). Of the 7 variables that exhibited different trends between the 2 groups, 5 variables (palatine length [PLL], BOW, FRL, PAW, and jugal length [JUL]) switched from a positive growth relationship with skull length to either a negative or, in the case of JUL, isometric trend (Table 3). The remaining 2 cases are represented by a prenatal to postnatal shift from negative to positive allometry for BSW and from negative allometry to isometry for PLW. Correspondence between prenatal and postnatal trends reduced to only 6 shared variables (35%) when LS results, using skull length, were compared. The 6 shared trends consisted of 3 positive trends, 2 isometrically scaled variables, and 1 negatively allometric trend, in all, reflecting the different growth trend results obtained for SQL, PRL, PRW, and PLL when using LS instead of RMA. When comparing the prenatal trends, derived using CRL, with postnatal trends, a similar pattern of more shared traits between prenatal RMA results and postnatal results is found. Eight growth trends are shared between prenatal and postnatal specimens when RMA results are compared. These include 4 positive, 2 negative, and 2 isometric trends. In contrast, when LS results are used, only 7 trends are shared with postnatal specimens, the difference being reflected by the identification of an isometric trend for PRW using RMA and a negative trend using LS (Table 3). Overall correspondence between RMA results derived from skull length and those derived using CRL is slightly higher (13 variables; 76%) than that between LS results for the same 2 groups (12 variables; 71%).

Multivariate results.—Principal component coefficients for both prenatal and postnatal specimens were reasonably robust, as indicated by bootstrapped *SE*s ranging from 0.008 (FRL) to 0.022 (basioccipital length [BOL]) for prenatal analyses and from 0.006 (SQL) to 0.019 (FRL and PAW) for postnatal analyses (Table 4). The proportion of variance accounted for by PC1 varied between 64% for the prenatal and 89% for the postnatal specimens (Fig. 3). Six isometric, 4 positive, and 4 negative trends were identified among prenatal specimens, and 7 negative, 5 positive, and 2 isometric trends were identified among postnatal individuals (Table 4). Prenatal and postnatal specimens shared only 5 (36%) of 14 growth trends, consisting of 3 positive trends (SQL, NAL, and PAL) and 2 negative trends (NAW and MIW; Fig. 4) These 5 variables also were found to have the same trends in the prenatal–postnatal comparison of bivariate results (Table 3).

For prenatal specimens 9 (64%) of the 14 variables analyzed using multivariate methods were found to have the same growth trend as indicated in bivariate analyses. The

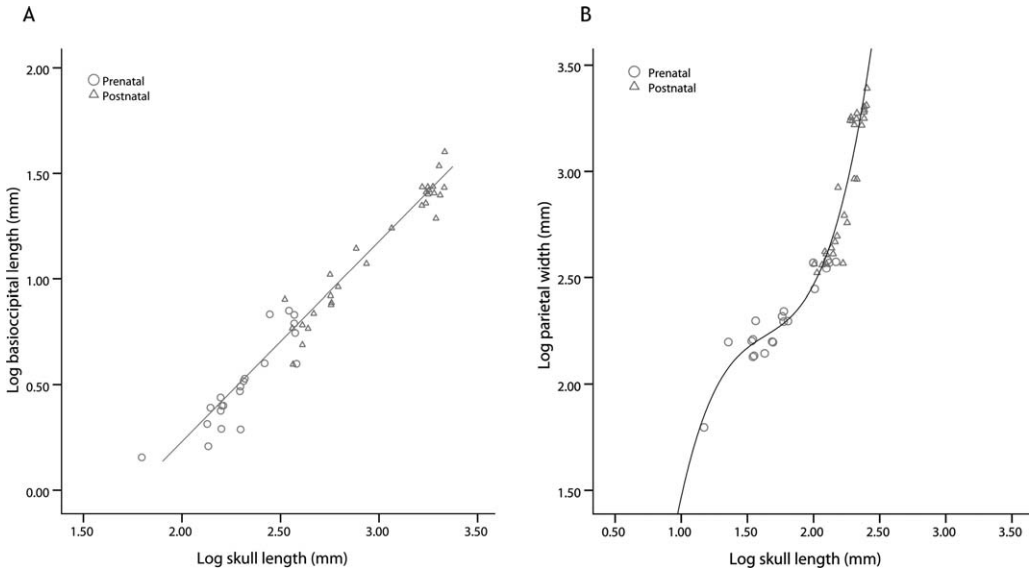

Fig. 2.—Comparison of prenatal and postnatal trajectories for relationships between skull length and A) parietal width and B) basioccipital length, using reduced major axis regression methods. Details of regression values are provided in Table 2.

differing growth trends were represented by 3 isometric trends that were identified as positively allometric under bivariate methods (PRL, FRL, and PAW) and 2 negative trends that were instead identified as isometric (PRW) and positive (MXL; Tables 3 and 4). Three of the 5 trends that differed between the 2 estimation methods (PRL, PRW, and MXL) also were found to differ between RMA and LS regression approaches (Table 3). For postnatal specimens 10 (71%) of 14 multivariate growth trends corresponded with their bivariate counterparts. Of the 4 trends that differed (JUL, MXL, BOL, and BOW), 2 negative trends were found to be isometric with bivariate methods (JUL and BOL), 1 positive trend was found to have a negative relationship (BOW), and 1 isometric trend was identified to be positively allometric using bivariate methods (MXL; Tables 3 and 4). The latter variable, maxilla length, was also the only one to differ between RMA and LS results for bivariate analyses (Table 3), with LS results corresponding to the multivariate estimate of isometry (Table 4).

Table 4.—Results of multivariate allometry analyses detailing principal component (PC) coefficients, bootstrap *SE* (in parentheses), and corresponding growth trend (GT) considering an isometric vector of 0.267 applicable to all variables (see ''Materials and Methods''). Symbols indicate isometry (=), positive allometry (+), and negative allometry (−). Definitions of osteological variables are provided in Table 1.

	Prenatal		Postnatal	
Variable	PC1 coefficient	GT	PC1 coefficient	GT
JUL	0.404 (0.021)	+	0.201 (0.010)	−
SQL	0.466 (0.019)	+	0.276 (0.006)	+
PRL	0.253 (0.019)	=	0.310 (0.010)	+
PRW	0.148 (0.011)	−	0.249 (0.019)	=
MXL	0.223 (0.009)	−	0.276 (0.010)	=
BOL	0.252 (0.022)	=	0.247 (0.018)	−
BOW	0.250 (0.018)	=	0.414 (0.011)	+
NAL	0.367 (0.008)	+	0.461 (0.009)	+
NAW	0.140 (0.009)	−	0.082 (0.011)	−
FRL	0.270 (0.008)	=	0.141 (0.019)	−
MIW	0.157 (0.020)	−	0.053 (0.018)	−
SKL	0.261 (0.017)	=	0.252 (0.011)	−
PAL	0.300 (0.009)	+	0.339 (0.010)	+
PAW	0.256 (0.019)	=	0.184 (0.019)	−

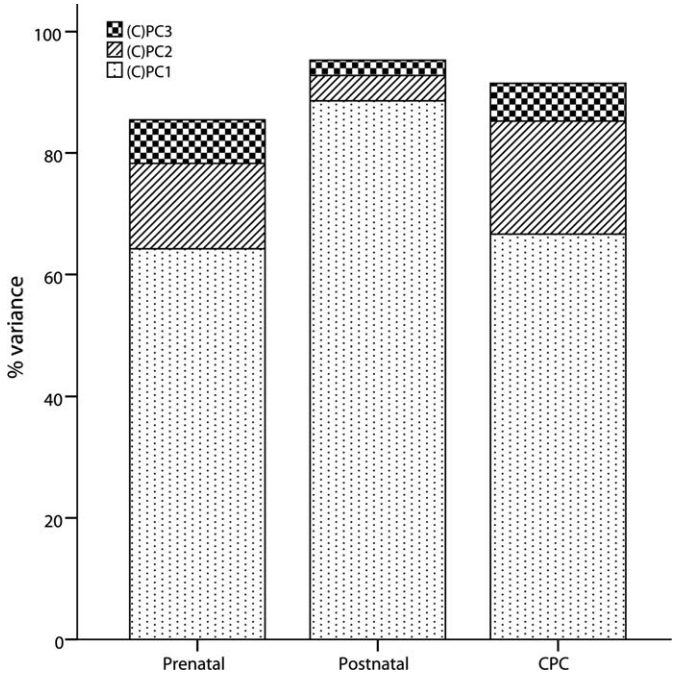

Fig. 3.—Eigenvalues, expressed as percentages of total variance, of principal component analysis of prenatal and postnatal matrices, and of the common principal component (CPC) analysis matrix, following the Flury hierarchy produced from CPC analysis of prenatal and postnatal matrices.

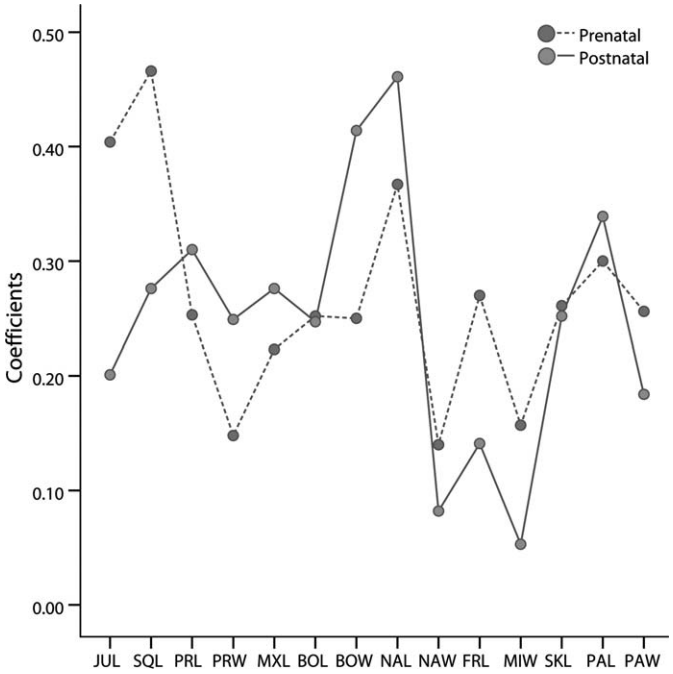

Fig. 4.—Comparison of prenatal and postnatal multivariate allometry estimated by principal component coefficients. Definitions of osteological variables (x axis) are provided in Table 1.

Matrix similarity tests and vector comparisons.—The comparison of CPC models with prenatal and postnatal matrices using random skewers provides an indication of how well the constrained matrices constructed under CPC analysis fit the actual matrices created from measurements of the prenatal and postnatal specimens. Pairwise comparisons between prenatal and postnatal matrices and the constructed matrices at each level of Flury's hierarchy are significant, indicating a close correspondence with the original data matrices (Table 5). The postnatal matrix is slightly more similar to the CPC matrices, on average (0.872), than the prenatal matrix (0.851), and both are most dissimilar in structure to CPC(1), with an average correlation of 0.869 (Table 5). The greatest discrepancies between the 2 original matrices and the CPC results are associated with the equality and proportionality models, with the postnatal matrix exhibiting a higher correlation to both models (0.968 and 0.981; Table 5) than the prenatal matrix (0.806 and 0.780; Table 5). This result is more marked when considering the vector angles between the PC1s of the matrices: when comparing the proportionality and equality matrices with the prenatal matrix, angular comparisons are 21° and 19°, respectively, but for postnatal matrix these values drop considerably to 3° and 4°, respectively. The result of overall similarity in patterns of covariance structure between the prenatal and postnatal matrices is further indicated by a significant correlation (0.69, $P = 0.008$) between the 2 matrices using a random skewers test and an angle measurement of 22.7° between the 2 PC1 vectors, which is smaller than expected between 2 random vectors (27.6°). The 1st principal component (CPC1) encapsulated the greatest amount of variance in the constructed CPC matrix (67%; Fig. 3). This was expected because both prenatal and postnatal PCAs yielded similar results. Nevertheless, in CPC analysis, unlike PCA, the largest proportion of variance might not be associated with the largest eigenvalue. To evaluate how much variance was associated with isometric and allometric variation the square of the inner product of the isometric vector and CPC1 vector was calculated. The proportion of isometric variation was 0.87, and hence the remaining 0.13 was due to allometry. The amount of variance expressed by CPC1 resulting from allometry (38%) was calculated by multiplying 0.13 by each of the eigenvectors of the CPC matrix and calculating a percentage for the 1st component. CPC1 variance for the equality matrix, which was the CPC model with the highest correlations with prenatal and postnatal matrices, was associated with NAL (21%) and BSL (23%), and SQL contributed the greatest proportion of variance to the CPC2 axis. NAL and BSL also exhibited positive allometric trends under bivariate analyses (RMA and LS) in both prenatal and postnatal specimens (Table 3).

Table 5.—Vector correlations from random skewers analysis for each pairwise comparison for the reconstructed covariance matrices at each step in the common principal components (CPC) analysis hierarchy: CPC = sharing of all principal components between the prenatal and postnatal matrices; CPC(1)–CPC(7) = sharing of a number of components, as denoted in the parentheses. All vector correlations are significant ($P < 0.008$).

	Prenatal	Postnatal	Average
Equality	0.806	0.968	0.887
Proportionality	0.780	0.981	0.881
CPC	0.851	0.872	0.862
CPC(7)	0.848	0.873	0.861
CPC(6)	0.849	0.872	0.861
CPC(5)	0.851	0.871	0.861
CPC(4)	0.851	0.871	0.861
CPC(3)	0.876	0.855	0.866
CPC(2)	0.899	0.842	0.870
CPC(1)	0.856	0.861	0.859

Discussion

Two broad conclusions can be reached from this study. First, prenatal and postnatal ontogenetic allometry differs, with the former being characterized by a comparatively increased rate of bone growth among several cranial variables, as evidenced by larger allometric coefficient values and a greater number of positive allometric trends. Second, the overall manner in which traits covary among prenatal and postnatal specimens is structurally similar, as indicated by high matrix correlations using random skewers tests at each stage of the CPC hierarchy.

Prenatal allometry is characterized in *R. pumilio* by a relative rapid lengthening of cranial elements, especially the frontal, parietal, basisphenoid, premaxilla, and palatine. Particularly, bivariate coefficients for parietal, palatine, and basisphenoid lengths were ≥30% greater for prenatal

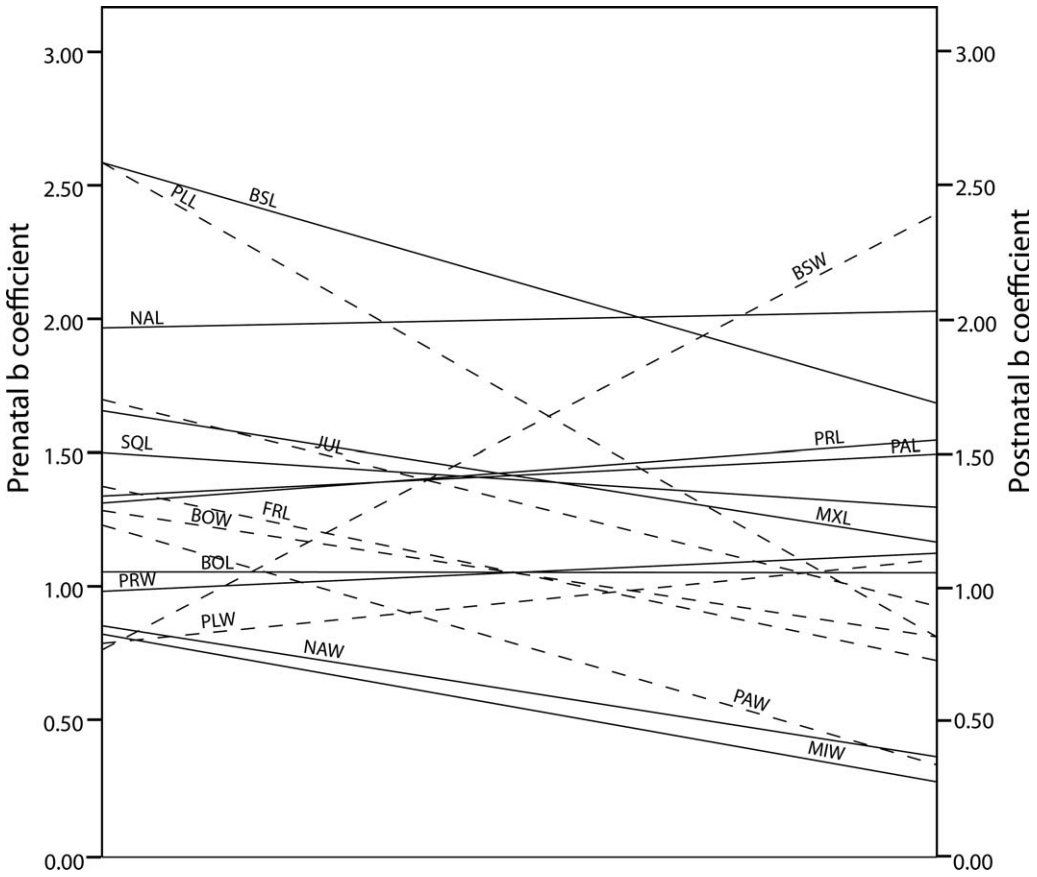

Fig. 5.—Prenatal and postnatal coefficients for each variable measured; abbreviations are as given in Table 1. Between the 2 periods a solid line represents a consistent allometric trend, and a dashed line represents a change in allometric trend. Absolute values plotted based on reduced major axis (RMA) regression using skull length, trends identified with bootstrapped confidence intervals.

compared to postnatal specimens (Fig. 5). The magnitudes of the prenatal coefficients in this study were comparable with the only other study of mammalian prenatal cranial allometry, which examines similar measurements to those taken herein, on the skull of the common European mole (0.7–4.5—Goswami and Prochel 2007). Coefficients for postnatal specimens were largely consistent with the range of values previously reported among allometry studies of other mammalian taxa, including rodents (0.2–2.3—Leamy and Atchley 1984, Leamy and Bradley 1982) and marsupials (0.4–1.5—Abdala et al. 2001, Flores et al. 2003). Notably, elements exhibiting a positive allometric trend are mostly those belonging to the neurocranial, as opposed to the facial, skeleton. Bivariate analyses indicate positive allometries are found for 6 of 8 neurocranial variables among prenatal specimens, and of these, frontal length and parietal width shift to display a negative allometry during postnatal ontogeny, indicating an alteration to a relatively reduced rate of bone growth in association with body size (Figs. 2B and 5). This overall trend of positive prenatal allometry supports the notion that during the prenatal period the brain is expanding rapidly and the neurocranial elements are thus growing quickly to encase and protect this organ (Herring 1993). Subsequently, postnatal growth of the neurocranium is typically isometric or negatively allometric to compensate for rapid prenatal growth and prevent distortion of the cranium in adulthood (Emerson and Bramble 1993), with neurocranial bone growth proceeding at sutural margins (Wilson and Sánchez-Villagra 2009). Another aspect of relevance is the timing of onset of ossification of the skeletal elements. This begins only around 4 days prior to birth in the house mouse (*M. musculus*—Kaufman 2008). A similar timing is expected for *R. pumilio*, based upon its close phylogenetic relatedness to *M. musculus* (Steppan et al. 2004) and because *R. pumilio* has a similar sequence of ossification in cranial elements to other muroid rodents (Wilson et al. 2010b). The accelerated growth of several prenatal elements herein is thus foreseeable, given the short period of time before birth for skeletal elements to grow.

With a more limited sample than presented here, Goswami and Prochel (2007) also were able to detect rapid prenatal bone growth in several elements, including the basisphenoid, frontal, and squamosal, as exhibited here for *R. pumilio*. The authors also noted that prenatal and postnatal growth trends for facial elements were more consistent with one another than for neurocranium elements. A similar trend is found among the variables analyzed herein, particularly for the nasal bone, which lengthens with positive allometry and widens with negative allometry throughout prenatal and postnatal ontogeny. The former feature is also consistent with nasal length allometric estimates for *T. europaea* (Goswami and Prochel

2007), and postnatal estimates of nasal length allometry in several marsupials, including *Didelphis albiventris* (Abdala et al. 2001), *Dromiciops gliroides* (Giannini et al. 2004), and *Caluromys philander* (Flores et al. 2010), also indicate a positive trend. In contrast with other marsupials and the rodent studied here, *Lutreolina crassicaudata* (Flores et al. 2003) and *Dasyurus albopunctatus* (Flores et al. 2006) did show negative or isometric trends, but those departures have been explained in connection with a greater dietary specialization (increased carnivory).

The shifts between prenatal and postnatal trends for some variables point to a nonlinearity of ontogenetic allometry in *R. pumilio*. Several authors have proposed postnatal ontogenetic allometry to be nonlinear in other rodent species (Hingst-Zaher et al. 2000; Zelditch et al. 1992). Particularly, Zelditch et al. (2003) have shown that both the house mouse (*M. m. domesticus*) and the cotton rat (*Sigmodon fulviventer*) have complex nonlinear trajectories, although these have been shown to stabilize shortly after weaning. The time of weaning represents a milestone in development that is associated with a major shift in dietary composition (Humphrey 2010) and has been suggested to exert an epigenetic impact on craniofacial morphology during growth (Helm and German 1996). Phenotypic variance decreases at around 35 days in mice (Atchley 1984; Riska et al. 1984; Willmore et al. 2006), and a broadly similar result has been found for the rat (*Rattus norvegicus*—Nonaka and Nakata 1984), suggesting that the effects of epigenetic influences have been determined already by this point and have little control on patterning variance in skull morphology (Willmore et al. 2006). The timing of development could play a role in the latter hypothesis, and Zelditch et al. (2003) suggested that stabilization of allometries can occur earlier in highly precocial mammals, perhaps even before birth. Based upon factors frequently used to ascribe either altricial or precocial development, such as birth weight and length of gestation period (Derrickson 1992; Martin and MacLarnon 1985), *R. pumilio* is considered, similar to many other muroids, to produce altrical neonates that wean at 16 days (Brooks 1982). However, in comparison to other muroids such as the house mouse that are described as altricial, *R. pumilio* weans around 5 days sooner. Similarly, the young of *R. pumilio* open their eyes after approximately 7 days, which is half-way between the time taken for young of *M. musculus* (14 days—Nowak 1999) and those of *Sigmodon* (0–1 days—Nowak 1999), an atypically precocial group of muroid rodents. Hence, it would be most probable that allometry stabilization occurs during postnatal development for *R. pumilio* and most likely slightly earlier than the timing indicated by Zelditch et al. (2003) for the house mouse, given the discrepancy in their life-history attributes. Nevertheless, the data presented herein suggest that birth represents a key point of transition for the growth dynamics of several cranial elements, especially the palatine, frontal, and parietal, but other elements such as the basisphenoid appear to display constant growth relationships across ontogeny. In a comparison of late prenatal and early postnatal ontogenetic allometry of the cranium in humans Sardi et al. (2007) found that some parts, such as the vault, exhibited differences in shape during ontogeny, but others, such as the facial region, did not. Examination of middle and late prenatal cranial ontogeny in humans and pigtailed macaques revealed similar trends (Zumpano and Richtsmeier 2003). The latter 2 studies, coupled with the results herein, suggest that morphological differentiation of some traits in the mammalian cranium is established during the prenatal period. Experimental studies have demonstrated that external stimuli can alter cranial form (Bouvier and Hylander 1981; Moore 1967; Smith 1981), indicating that morphogenesis of the skull is affected by epigenetic factors and genetic factors. The shift in growth dynamics at birth for several of the elements measured herein promotes epigenetic control of bone growth, because if an exclusively genetic program was followed, one would not anticipate a shift at birth, which marks the point when epigenetic factors, assumed here to be defined as all stimuli affecting skull growth as per Hall (1983), are likely to begin asserting a greater degree of regulation on skull growth (Rayne and Crawford 1972). A complex organization of cranial growth is evident, and further consideration of the influence of birth upon cranial growth dynamics clearly is warranted.

In a broad study of postnatal growth for muroid and hystricognath species Wilson and Sánchez-Villagra (2010) demonstrated that changes in covariance structure, as denoted by alterations to PC1 axes, are common among rodents. The intertrajectory angle of 22.7° found herein between prenatal and postnatal stages of *R. pumilio* falls within the range of vector angles that Wilson and Sánchez-Villagra (2010) reported between species (7.7°–33.1°), suggesting that ontogenetic allometric variation is of a similar magnitude to evolutionary allometric variation. Although the sample size of Goswami and Prochel (2007) did not permit a vector comparison between prenatal and postnatal allometry, the results of Zelditch et al. (2003) indicated large and statistically significant differences in vector angles between successive stages during the postnatal ontogenies of *M. m. domesticus* (up to 73.5°) and *S. fulvivienter* (up to 84.6°). In comparison to the latter study, the closer correspondence between prenatal and postnatal specimens could be due to the effects of a general size factor, as previously suggested by Cheverud (1982) in relation to concordance between static and ontogenetic allometry. The latter might be further exacerbated because all of the measurements herein are either lengths or widths of elements, whereas in the work of Zelditch et al. (2003) geometric morphometric landmarks were recorded on the rodent crania.

Despite the differences between prenatal and postnatal allometry trends identified in the bivariate analyses, the overall composition of the 2 covariance matrices is significantly similar, as shown by the correlations between the original and CPC matrices using random skewers. CPC analysis partitions variance in the same manner as PCA, onto orthogonal axes. If the factor causing covariation structure is limited largely to a similar orthogonal axis, for instance in the case here of multivariate allometry where the PC1 reflects a

general size axis to which other variables are highly correlated, it is likely that CPC analysis will result in the construction of a shared matrix that is significantly correlated with the originals. One thing to consider with this scenario is the biological reality of orthogonal structure, particularly as Houle et al. (2002) have cautioned against the interpretation of CPC results in terms of biological causation. Nevertheless, this is also a relevant criticism of PCA, which assumes uncorrelated orthogonal axes, and because PC1 here reflects general size, PC2 represents a contrast of 2 ways to attain size and by definition is correlated to PC1 (see Mitteroecker et al. [2005] for discussion of PCA). Using an analogous approach to that applied herein, in their study of Neotropical primates Cheverud and Marroig (2007) also found high pairwise correlations between CPC-constructed matrices at each stage of the hierarchy (range: 0.943–0.990). Also CPC analysis has been used in studies of several nonmammalian taxa and has indicated shared composition between and within types of allometry among (Klingenberg 1996; Klingenberg and Zimmermann 1992) and within (Cuzin-Roudy 1975) species. Studies on differences in postnatal covariance structure of cranial variables among rodents have yielded some results of similarity among populations of muroid rodents, including between members of the genus *Zygodontomys* (Voss et al. 1990) and also *Phyllotis* (Steppan 1997), but differences have been found between static and ontogenetic allometries for *M. musculus* (Leamy and Bradley 1982), within stages of ontogenetic allometry for the hystricognath rodent *Thrichomys apereoides* (Monteiro et al. 1999), and for the muroid rodent *Mastomys natalensis* (Fadda and Leirs 2009). Evaluating the significance of the highly similar prenatal and postnatal matrices is difficult because the aforementioned studies of rodents all examined postnatal growth and methodological limitations have been noted in association with CPC analysis. It has been shown that small sample sizes do influence CPC results, mostly in favor of accepting a similar structure between matrices (Houle et al. 2002; Marroig and Cheverud 2001). The random skewers test used in this study is a more robust method. Because randomization is achieved through the application of random selection vectors to each matrix rather than the randomization of the columns and rows of the original matrices, it reduces the potential influence of sample size bias to the statistical significance of the outcome. However, matrices containing well-separated eigenvalues tend to have more influence on CPC analysis than do those with eigenvalues that are almost equal to one another (Airoldi and Flury 1988). This could explain why the postnatal matrix corresponds more closely to the CPC-constructed matrices than the prenatal matrix, as indicated by much narrower vector angles and higher random skewers correlations in relation to the equality and proportionality models (Table 5). Because the age range encapsulated within the postnatal sample exceeds that of the prenatal one, and PC1, in accordance with multivariate allometry, largely accounts for size variation, the relative magnitude of the 1st eigenvector in relation to the succeeding ones is greater for the postnatal matrix than the prenatal matrix and as such exerts a greater influence on CPC analyses.

This study compared prenatal and postnatal ontogenetic allometry in the African striped mouse (*R. pumilio*). Results indicate that the prenatal period is characterized by rapid bone growth, as evidenced by larger bivariate allometric coefficients and a greater proportion of cranial elements growing with a positive allometry than in the postnatal period. Growth dynamics are found to shift for measurements of several elements including the parietal, frontal, and palatine, indicating a nonlinearity of ontogenetic allometry with respect to birth. CPC and random skewers results demonstrate that the prenatal and postnatal matrices are structurally highly similar, indicating that covariance structure is conserved over ontogeny. Further empirical study to unravel the role prenatal allometry plays in the generation of adult form undoubtedly will provide greater insight into the dynamics of ontogenetic allometry.

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